



Review of metazoan parasites of the northern fur seal (*Callorhinus ursinus*) and the analysis of the gastrointestinal helminth community of the population on St. Paul Island, Alaska

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Abstract

The northern fur seal (NFS), *Callorhinus ursinus* (Mammalia: Otariidae), is a marine mammal species included into the IUCN Red List as the vulnerable species which population is dramatically declining. A significant amount of parasitological data collected previously and our recent data allowed us to clarify the list of NFS metazoan parasites and to perform a comprehensive analysis of the gastrointestinal helminth community. Gastrointestinal tracts from 756 NFSs (3- to 4-year-old males) were collected during the annual Aleut subsistence harvests in July–August of 2011–2014 from five separate rookeries on St. Paul Island, Alaska. Totally, 27,625 specimens of helminths and approximately 1000 nasal mites were collected and identified. Detailed analysis of the previously published and newly obtained data revealed 32 species of metazoan parasites, including trematodes (6 species), cestodes (4), nematodes (9), acanthocephalans (9) and arthropods (4). The gastrointestinal helminth community of newly studied NFSs comprised 19 species including trematodes (4), cestodes (3), nematodes (5) and acanthocephalans (7). Temporal changes in the helminth community structure were small but statistically significant. Gastrointestinal helminth infracommunities comprised from 1 to 10 species (average of 4). Small but significant correlation was found between the abundances of acanthocephalans (*Corynosoma similis* and *C. strumosum*), nematodes (*Contracaecum osculatum*, *Pseudoterranova* spp.) and cestode *Diphyllobothrium tetrapterum*.

Keywords Acanthocephala · Cestoda · Nematoda · Trematoda · Marine mammals · Parasite community

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Introduction

The northern fur seal (NFS), *Callorhinus ursinus* Linnaeus, 1758 (Mammalia: Otariidae), is the only living species of the genus *Callorhinus* Gray, 1859. The distribution of NFS includes breeding areas in the North Pacific extending from the Kuril Islands of Russia, across the Bering Sea and south to the west coast of the USA with the southernmost rookery on San Miguel Island, the most western island in the Channel Islands of Southern California. The global NFS population was estimated to be approximately 1.29 million in 2014. This estimation reflects a decline of NFS population by approximately 658,000 from 1976, resulting in the NFS's IUCN Red List categorization as a Vulnerable species under criterion A2b (Gelatt et al. 2015). The largest breeding rookeries of the NFS are now located on St. Paul Island, Pribilof Archipelago, Alaska (Gelatt et al. 2015). In the past, the Pribilof Archipelago represented approximately 75% of the

world's NFS population. Current metrics indicate that the Pribilof Archipelago's population has declined by approximately 66% over the last three generations (1972–2014) with an annual 5.5–5.8% decline in pup production (Towell et al. 2006; Allen and Angliss 2015; Gelatt et al. 2015). Several hypotheses have been proposed to explain the causes for this decline that include predation, human interactions (e.g. by-catch, entanglement, ship disturbance, pollution) and food limitations. However, due to insufficient data on population vital rates, prey resources and potential causes of mortality, the exact reason behind the decline in NFS pup production is unknown (Trites 1992; NMFS 2007). Prior multi-year studies conducted on St. Paul Island have not shown specific bacterial, viral or parasitic diseases to be responsible for reducing the NFS population. Rather, emaciation and trauma were reported to be the primary causes of NFS mortality of pre-weaned pups (Spraker and Lander 2010).

Studies on NFS biology and ecology including their parasites and diseases have been performed in different localities for more than 100 years (Scott et al. 2006; Felix 2013). The historically first parasites reported from NFSs were anisakid nematodes discovered in pups on St. Paul Island in 1879 by Dr. White (see Scheffer et al. 1984). Later, Stiles and Hassall (1899) identified the nematodes *Ascaris decipiens* Krabbe, 1878 (now *Pseudoterranova decipiens*), *Uncinaria* sp. (now *Uncinaria lucasi* Stiles 1901) and the cestode *Bothriocephalus* sp. (now *Adenocephalus pacificus* Nybelin, 1931). The louse *Echinophthirius callorhini* Osborn 1899 (now *Antarctophthirus callorhini*) was described in the same year from NFS collected on Pribilof Archipelago. Later, Delyamure (1961) reported 21 helminth species from NFSs located on the Commander Archipelago. Since then, more than 40 species of metazoan parasites have been documented in NFSs in various parts of their range (Delyamure 1955, 1961; Dailey and Brownell 1972; Margolis and Dailey 1972; Dailey 1975; Yurakhno 1998; Felix 2013). Recent studies of anisakid nematodes based on molecular methods have revealed that the most common species, *Anisakis simplex* (Rudolphi, 1809), *Pseudoterranova decipiens* and *Contracaecum osculatum* (Rudolphi, 1802) are “species complexes” and include several morphologically indistinguishable cryptic species (Mattiucci and Nascetti 2008; Mattiucci et al. 2014, 2018). Therefore, at present, it is almost impossible to determine the precise number of species parasitizing NFSs. Moreover, it is extremely complicated to plan and perform a comprehensive parasitological investigation of NFSs due to the IUCN Red List of Threatened Species protections (Gelatt et al. 2015), which create an impasse in obtaining official permissions for the dissection of a significant number of NFSs for scientific purposes.

Most of the parasitological studies of NFSs on the Pribilof Archipelago were carried out between 1950 and 1970 and predominantly addressed *Uncinaria lucasi* (Olsen 1958;

Olsen and Lyons 1962; Lyons 1963;) or *Acanthocheilonema* (*Dipetalonema*) *odendhali* (Perry, 1967) (Perry and Forrester 1971); however, these studies were based on occasional examinations of a small number of seals (Neiland 1961; Keyes 1965). Extensive studies of NFS parasites were carried out between 1960 and 1980 in the former USSR, mainly on the Commander and Kuril Archipelagos (Delyamure and Skrjabin 1960; Delyamure 1961; Chupakhina 1971; Timofeeva et al. 1972; Kovalenko 1975; Yurakhno and Taikov 1986; Yurakhno 1998). Recent studies have been carried out exclusively on St. Paul Island (Lyons et al. 2000, 2011, 2012, 2014; Ionita et al. 2008; Kuzmina et al. 2012, 2013, 2014, 2015, 2018).

The primary objective of this study was to review the published literature data addressing parasites of NFSs and to update the list of metazoan parasites with the inclusion of new data. Parasitological data collected during the last decade allowed us to perform a comprehensive analysis of the gastrointestinal helminth community of NFSs from St. Paul Island both at infracommunity and component community levels. Additionally, we hypothesized the existence of spatial and temporal differences in the gastrointestinal helminth community and tested the assumption using a linear model approach.

Material and methods

Collecting and identification of the material

This study was carried out on St. Paul Island (57° 09' N, 170° 13' W), Alaska, USA, in July–August of 2011–2014. Gastrointestinal tracts from 756 NFS males 3–4 years of age including additional organs were collected during the annual Aleut subsistence harvests from five separate haul-out areas adjacent to the five rookeries: Gorbatch ($n = 125$), Lukanin ($n = 165$), Morjovi ($n = 120$), Polovina ($n = 164$) and Zapadni ($n = 182$) (see map in our previous studies, Kuzmina et al. 2015, 2018).

Each gastrointestinal tract was separated into three parts (stomach, small intestine, large intestine), then dissected and examined according to Bowman and Lynn (1995). Intestinal content was collected separately from each segment of the digestive system and washed through 50 mesh sieves (0.297 mm) to collect small helminths. All parasites were collected manually under a dissecting microscope, washed in saline, and fixed in 70% non-denatured ethanol. A total of 27,625 specimens of helminths were collected and identified. Tapeworms were immediately killed through immersion in hot water, after which they were placed into 70% non-denatured ethanol. Before identification, all nematodes were cleared in lactophenol (25% phenol, 25% lactic acid, 25% glycerine and 25% distilled water) for approximately 3 h. Trematodes were clarified in lactophenol for 30 min before

identification. Selected specimens of trematodes and cestodes were stained with acetocarmine, dehydrated in a graded ethanol series, cleared in clove oil, mounted permanently in Canada balsam and identified under a light microscope using morphological criteria (see Hernández-Orts et al. 2015; Kuzmina et al. 2018). All acanthocephalans were mounted in Berlese's medium, examined and morphologically identified under light microscope Zeiss Axio Imager M1 (Kuzmina et al. 2012). Selected heads of 37 NFSs and additional internal organs of several NFSs were also examined for metazoan parasites. Mites were collected from NFS nasal cavities and nematodes were collected from the lungs and pelt subcutaneous tissues. All collected parasites were fixed in ethanol and identified by their morphology.

Morphological vouchers of studied metazoan parasites were deposited in the parasitological collection of the I. I. Schmalhausen Institute of Zoology NAS of Ukraine (Kyiv, Ukraine), the Helminthological Collection of the Institute of Parasitology, Czech Academy of Sciences (IPCAS) (České Budějovice, Czech Republic) and the National Museum of Natural History, Smithsonian Institution (USNM) (Washington, D.C., USA) (Kuzmina et al. 2012, 2014, 2015, 2018).

Data analysis

The prevalence (P), mean abundance (MA) and mean intensity (I) were calculated for each helminth species following the definitions of Bush et al. (1997). The relative abundance (RA) was calculated as the ratio (percentage) of the number of specimens of a particular species to the total number of helminth specimens in the sample. The analysis of the gastrointestinal helminth community was performed using only the complete gastrointestinal helminth collections from 651 of the 756 hosts examined in 2012–2014.

The calculations were performed using R software v. 3.6.1–3.6.3 (R Core Team 2020). Two packages were used in addition to the standard R packages: RRPP v. 0.6.0. (Collyer and Adams 2018, 2019) and corplot v. 0.84 (Wei and Simko 2017). Effects of rookery and year were tested using linear model evaluation with a randomized residual permutation procedure realized in the *lm.rpp* function of the R package RRPP. In total, 9999 permutations were used for testing.

Since our task was to evaluate the territorial and temporal variation in the levels of infection, we considered the set of annual estimates of the infection level in the studied rookeries as a sample from a great number of localities at different points of time. Therefore, the effects of rookery were treated as a random effect in the analysis, as well as the effect of the year. If the differences between the levels of infection between the rookeries occurred to be significant, one could make the pairwise comparisons of the levels of infection in different

rookeries and describe the differences by multidimensional scaling or by an appropriate alternative technique. In our testing, significant differences between the rookeries did not occur (see the “Results” section below). Therefore, we did not conduct additional analyses through multidimensional scaling or other means.

To assess whether the gastrointestinal helminths of different taxa tend to occur together, the correlations between their numbers were analysed using the Spearman's correlation coefficient (r_s). The number of intestinal helminths of a certain taxon in the infracommunity of NFS was treated as a quantitative character, and the number of specimens of helminths of this taxon found in one individual of NFS was used as a value of this character for the individual. The p values of the obtained correlation coefficients were corrected for multiple comparisons by the Benjamini–Yekutieli method (Benjamini and Yekutieli 2001) conducted using the R function *p.adjust*. To find the sets of correlated characters, we applied the hierarchical cluster analysis realized in the R function *hclust*. We used $(1 - r_s)$ as the distance measure and the single linkage method as the clustering technique. To visualize the results, the R function *hclust* and the R package *corrplot* were used.

Results

Review of metazoan parasites of *Callorhinus ursinus*

Detailed analysis of the published data, including our previous studies, revealed 33 species documented as valid metazoan parasites of NFS, including 29 species of helminths (7 trematodes, 4 cestodes, 9 nematodes and 9 acanthocephalans) and 4 species of parasitic arthropods (Table 1; Fig. 1). Two species of trematodes, *Apophallus (Pricetrema) callorhini* (Yurakhno 1986) and *Cryptocotyle (Ciureana) delamurei* (Yurakhno 1987), were identified once in one NFS from the Commander Archipelago (Yurakhno 1986, 1987) (Fig. 1). Tatonova and Besprozvannykh (2019) listed the latter species as valid. A third trematode reported in NFS is the heterophyid *Cryptocotyle jejuna* (Nicholl, 1907) (Keyes 1965; Neiland 1961), a common parasite of European birds. The validity of these three species in NFS is questionable in the relation of other similar small trematodes reported from NFS. A recent extensive study by Kuzmina et al. (2018) molecularly confirmed two heterophyids (*Phocitrema fusiforme* Goto and Ozaki, 1930, *Galactosomum ubelakeri* (Dailey, 1969)) and one troglotrematid *Nanophyetus salmincola* (Chapin, 1926) infecting NFS on St. Paul Island. Seven species of tapeworms have been recognized in NFSs by Yurakhno (1998). However, only one immature tetrabothriid, two adult diphyllobothriids, and an accidental infection of cestode larvae (*Scolex pleuronectis*) that might belong to the larval type I of Jensen and Bullard (2010) and corresponds with members

Table 1 Checklist of metazoan parasites reported from northern fur seal (*Callorhinus ursinus*) in published records and in this study (in bold)

Species	Host / S ¹	Records in NFS
TREMATODA		
1 <i>Apophallus zalophi</i> Price, 1932	CSL / I	Neiland 1961; Keyes 1965; Yurakhno 1986; Kuzmina et al. 2018
2 <i>Apophallus callorhini</i> ² (Yurakhno 1986) (?)	NFS/I	Yurakhno 1986
3 <i>Cryptocotyle delamurei</i> ³ (Yurakhno 1987) (?)	NFS / I	Yurakhno 1987
4 <i>Cryptocotyle jejuna</i> (Nicholl, 1907) (?)	bird / I	Keyes 1965; Neiland 1961
5 <i>Galactosomum ubelakeri</i> (Dailey, 1969)	CSL / I	Kuzmina et al. 2018
6 <i>Nanophyetus salmincola</i> (Chapin, 1926)	dog / I	Kuzmina et al. 2018
7 <i>Phocitrema fusiforme</i> Goto et Ozaki, 1930	RS / I	Afanasev 1941; Neiland 1961; Keyes 1965; Kuzmina et al. 2018
CESTODA		
8 <i>Anophryocephalus ochotensis</i> Delyamure et Krotov, 1955	SSL / I	Yurakhno and Taikov 1986; Kuzmina et al. 2015
9 <i>Adenocephalus pacificus</i> ⁴ Nybelin, 1931	JFS / I	see Hernández-Orts et al. 2015
10 <i>Diphyllobothrium tetrapterum</i> ⁵ (Siebold, 1848)	seal / I	see Hernandez-Orts et al. 2018
11 <i>Scolex pleuronectis</i> ⁶	whale / I	Chupakhina 1971; Yurakhno and Taikov 1986; Skrjabin and Yurakhno 1972
NEMATODA		
12 <i>Acanthocheilonema odendhali</i> ⁷ (Perry, 1967)	CSL / T	Delyamure 1961; Keyes 1964; Nikolskij 1969; Perry and Forrester 1971; Machida 1977; Kagei and Oda 1975; Yurakhno and Taikov 1986; Kuzmina et al. 2013
13 <i>Anisakis simplex</i> s. l. (Rudolphi, 1809)	PP / S	Delyamure and Skrjabin 1960; Machida 1969; Kovalenko 1975; Yurakhno and Taikov 1986; Gerber et al. 1993; Nagasawa 1999; Kuzmina et al. 2014
14 <i>Anisakis physeteris</i> (Baylis, 1923) (?)	whale / S	Nagasawa 1999
15 <i>Contracaecum osculatum</i> s. l. (Rudolphi, 1802)	HS / S	Yamaguti 1951; Margolis 1956; Delyamure and Skrjabin 1960; Keyes 1965; Machida 1969; Yurakhno and Taikov 1986; Gerber et al. 1993; Kuzmina et al. 2014
16 <i>Parafilaroides decorus</i> Dougherty et Herman, 1947	CSL / L	Gerber et al. 1993
17 <i>Phocascaris cystophorae</i> ⁸ (Berland, 1963)	CC / I	Yurakhno and Taikov 1986; Kuzmina et al. 2014
18 <i>Pseudoterranova decipiens</i> s. l. (Krabbe, 1868)	PG / S	Stiles and Hassall 1899; Afanasev 1941; Yamaguti 1951; Fisher 1952; Krotov and Delyamure 1952; Delyamure 1955; Margolis 1956; Neiland 1961; Machida 1969; Kuzmina et al. 2014
19 <i>Pseudoterranova azarazi</i> (Yamaguti et Arima, 1942)	PF / S	Delyamure and Skrjabin 1960; Machida 1969; Skrjabin and Yurakhno 1972; Kuzmina et al. 2014
20 <i>Uncinaria lucasi</i> Stiles 1901	NFS / I	Stiles and Hassall 1899; Stiles 1901; Delyamure 1955; Olsen 1958; Olsen and Lyons 1962; Keyes 1965; Chupakhina 1971; Lyons et al. 2000, 2011, 2012; Ionita et al. 2008
ACANTHOCEPHALA		
21 <i>Bolbosoma nipponicum</i> ⁹ Yamaguti, 1939	NFS / I	Krotov and Delyamure 1952; Delyamure 1955; Petrochenko 1958; Delyamure and Skrjabin 1960; Machida 1969; Kuzmina et al. 2012
22 <i>Corynosoma alaskensis</i> Golvan, 1959	PP / I	Kuzmina et al. 2012
23 <i>Corynosoma cameroni</i> Van Cleave 1953	BW / I	present study
24 <i>Corynosoma semerme</i> (Forsell, 1904)	RS / I	Van Cleave 1953; Petrochenko 1958; Kovalenko 1975; Ionita et al. 2008 ¹⁰ ; Kuzmina et al. 2012; Lisitsyna et al. 2019
25 <i>Corynosoma similis</i> Neiland 1962	NFS / I	Neiland 1962; Kuzmina et al. 2012
26 <i>Corynosoma strumosum</i> (Rudolphi, 1802)	HS / I	Van Cleave 1953; Petrochenko 1958; Neiland 1961; Ionita et al. 2008; Kuzmina et al. 2012; Lisitsyna et al. 2019
27 <i>Corynosoma validum</i> Van Cleave 1953	PW / I	Ionita et al. 2008; Kuzmina et al. 2012; Lisitsyna et al. 2019
28 <i>Corynosoma villosum</i> Van Cleave 1953	SSL / I	Van Cleave 1953; Petrochenko 1958; Yurakhno and Taikov 1986; Kuzmina et al. 2012; Lisitsyna et al. 2019
29 <i>Corynosoma ventronudum</i> Skrjabin, 1959	SSL / I	Delyamure and Skrjabin 1960
ARTHROPODA		

Table 1 (continued)

Species	Host / S ¹	Records in NFS
30 <i>Antarctophthirus callorhini</i> ¹¹ (Osborn 1899)	NFS / Sk	Osborn 1899; Afanasev 1941; Jellison 1952; Keyes 1965; Miller 1971; Kim and Chung 1972
31 <i>Orthohalarchne attenuata</i> (Banks 1910) Newell, 1947	NFS / N	Banks 1910; Oudemans 1926; Keyes 1965; Machida 1969; Nagasawa 1999
32 <i>Orthohalarchne diminuata</i> Doetschman 1944	CSL / L	Doetschman 1944; Keyes 1965; Machida 1969; Nagasawa 1999
33 <i>Proechinophthirus fluctus</i> ¹² (Ferris, 1916)	SSL / Sk	Ferris 1934, 1951; Ewing 1923; Jellison 1952; Keyes 1965; Blagoveschenskij 1966; Miller 1971; Kim and Chung 1972; Timofeeva et al. 1972

References from checklists of Delyamure (1955), Dailey and Brownell (1972), Margolis and Dailey (1972), Dailey (1975), Yurakhno (1998) and Felix (2013) were not included into the list

¹ Type host/site of infection in NFS: I — intestine, L— lungs, N— nasal cavity, S— stomach, Sk— skin, T subcutaneous tissues, bird — *Totanus calidris*, BW — *Delphinapterus loucas*, dog — *Canis familiaris*, CC — *Cystophora cristata*, CSL — *Zalophus californianus*, HS — *Phoca vitulina*, JFS — *Arctocephalus philippii*, NFS — *Callorhynchus ursinus*, PF — *Phoca fasciata*, PG — *Phoca groenlandica*, PP — *Phocoena phocoena*, PW — *Odobenus rosmarus*, RS — *Phoca hispida*, SSL — *Eumetopias jubatus*, whale — *Physeter microcephalus*

² (as *Pricetrema*)

³ (as *Ciureana*)

⁴ (syn. *Diphyllobothrium pacificum*); reported also as *Diphyllobothrium hians*, *D. lanceolatum* or *Pyramicocephalus phocarum*

⁵ (syn. *Diplogonoporus violetteae*; reported also as *Diphyllobothrium hians*, *D. lanceolatum* or *Pyramicocephalus phocarum*)

⁶ Larval type I (Onchoproteocephalidea) by Jensen and Bullard (2010)

⁷ (syn. *Dipetalonema odendhali*); Nagasawa (1999) probably misidentified with *Dirofilaria immitis* (Leidy, 1856)

⁸ (syn. *P. phocae*)

⁹ (syn. *B. bobrovoi*)

¹⁰ Misidentified with *C. obtuscens* (see Lisitsyna et al. 2019)

¹¹ (as *Haematopinus*)

¹² (as *Echinophthirus*)

(?) Questioned records that need verification

of the order Onchoproteocephalidea from elasmobranchs were confirmed as valid parasites of NFS (see Table 1). We found 7 of 8 nematode species confirmed as valid parasites of NFS (Table 2), but only 5 were included in the present analyses, due to their inhabitation of the gastrointestinal tract. *Anisakis physeteris* (Baylis, 1923) is a parasite of sperm whales, but its single report from an NFS in Japan was most probably a misidentification or an accidental finding (Nagasawa 1999). Finding microfilaria and identifying them as *Dirofilaria immitis* (Leidy, 1856) in NFSs also was reported by Nagasawa (1999). This was an unusual finding of a well-known dog parasite and most likely a misidentification with *Acanthocheilonema odendhali* (Perry, 1967). All 9 species of acanthocephalans reported from NFSs are considered as valid. We confirmed the presence of 7 species, including *Corynosoma cameroni* Van Cleave 1953, reported from NFSs for the first time (Kuzmina et al. 2012).

From the 37 NFS heads examined, a total of approximately 1000 nasal mites were found. The greatest intensity of mite infection within an NFS head was 226 specimens, including

larval stages. Specific studies of nasal mites were not performed. Additionally, the nematode *Acanthocheilonema odendhali* was found in subcutaneous tissues of 89 of 502 NFS examined (17.83%). *Uncinaria lucasi* was found in 9 NFS pups (see Lyons et al. 2012, 2014).

Orthohalarchne attenuata (Banks 1910) was documented in the nasal cavity of all 37 NFSs. Several individuals of *O. diminuata* Doetschman 1944, were found in the lower trachea of 6 seals. Two other dermal louse species previously reported from NFSs were not found, likely due to the absence of skin examination in this study. Yurakhno (1998) reported 2 species of ticks, *Ceratixodes arcticus* (Osborn 1899) (now *Ixodes stignatus* Birula, 1895) and *Hyaloma puta* (Pickard-Cambridge, 1876) (now *I. uriae* White, 1852) from NFSs, but these species are parasites of birds and their finding might represent accidental infections.

Based on this critical study, we confirmed only nematode (*Uncinaria lucasi*), anoplura (*Antarctophthirus callorhini*) and two trematodes (*A. callorhini* and *C. delamurei*) as specific parasites of NFS. All other metazoan parasites reported

Table 2 Gastrointestinal helminths found in northern fur seals *Callorhinus ursinus* on St. Paul Island, Alaska, USA. Prevalence (P) is shown with 95% confidence interval in parentheses; mean intensity (I) is followed by minimum and maximum values in parentheses; abundance is shown as mean (MA) and relative abundance (RA; a percentage of a species in the total number of helminth specimens)

	Species	Site of infection	P, %	I	MA (RA)
	TREMATODA				
1	<i>Apophallus zalophi</i>	SI	1.4 (0.7–2.6)	3.7 (1–9)	0.05 (0.14%)
2	<i>Galactosomum ubelakeri</i>	SI	4.8 (3.4–6.7)	10.7 (1–127)	0.5 (1.4%)
3	<i>Nanophyetus salmincola</i> *	SI	0.2 (0.02–0.9)	1540	NC
4	<i>Phocitrema fusiforme</i>	SI	28.0 (24.6–31.6)	10.1 (1–410)	2.8 (7.8%)
	CESTODA				
5	<i>Adenocephalus pacificus</i>	C, LI	97.2 (95.6–98.3)	18.5 (1–107)	18.0 (49.7%)
6	<i>Anophryocephalus ochotensis</i>	C	0.6 (0.2–1.6)	1.2 (1–2)	0.01 (0.02%)
7	<i>Diphyllobothrium tetrapterum</i>	C, LI	43.6 (39.9–47.5)	5.1 (1–29)	2.2 (6.1%)
	NEMATODA				
8	<i>Anisakis simplex</i>	S	43.6 (39.9–47.5)	8.1 (1–265)	3.6 (9.8%)
9	<i>Contraecum osculatum</i>	S	45.5 (41.6–49.3)	3.6 (1–39)	1.6 (4.6%)
10	<i>Pseudoterranova decipiens</i> **	S	84.2 (81.1–86.8)	6.5 (1–63)	5.5 (15.2%)
11	<i>Pseudoterranova azarazi</i> **	S			
12	<i>Phocascaris cystophorae</i>	S, IN	5.5 (4.0–7.6)	1.8 (1–7)	0.1 (0.3%)
	ACANTHOCEPHALA				
13	<i>Bolbosoma nipponicum</i>	IN	3.5 (2.3–5.3)	1.5 (1–11)	0.05 (0.15%)
14	<i>Corynosoma strumosum</i>	IN	24.0 (20.8–27.4)	2.9 (1–30)	0.7 (1.9%)
15	<i>Corynosoma cameroni</i>	IN	0.9 (0.4–2.0)	1.0 (1.0–1.0)	0.01 (0.03%)
16	<i>Corynosoma semerme</i>	IN	15.2 (12.6–18.2)	2.0 (1–10)	0.3 (0.9%)
17	<i>Corynosoma similis</i>	IN	15.8 (13.2–18.9)	3.2 (1–26)	0.5 (1.4%)
18	<i>Corynosoma validum</i>	IN	1.7 (0.9–3.0)	1.5 (1–3)	0.03 (0.07%)
19	<i>Corynosoma villosum</i>	IN	13.8 (11.3–16.7)	1.4 (1–9)	0.2 (0.5%)

*Species was not included in the analysis of helminth community; **two *Pseudoterranova* species were combined in calculations; NC not calculated. Site of infection: S – stomach, SI – small intestine, IN – intestine, C – caecum, LI – large intestine

from NFSs are known from other pinnipeds, or even from terrestrial mammals and birds (Table 1).

Composition and structure of the component community of gastrointestinal helminths

In total, 19 species of gastrointestinal helminths collected from 651 NFSs were included in the community analysis. Cestodes were the most abundant taxonomic group and represented more than half of collected parasites (53%; 14,660 specimens; 2 species), followed by nematodes (29%; 7894; 5 species) and trematodes (14%; 3867; 4 species). The acanthocephalans were less abundant and composed only 4% (1204; 7 species) of all intestinal helminths (Table 2).

Acanthocephalans were represented by 7 species of the family Polymorphidae. Their total occurrence was comparatively low; 47.3% of the hosts harboured at least one acanthocephalan species, but none of the species had a mean abundance higher than 1.0. The highest intensity of infection was observed in *Corynosoma strumosum* (Rudolphi, 1802) with up to 30 specimens in one NFS, and *C. similis* Neiland 1962, up to 26 specimens (Table 2). One specimen of *C. cameroni*

was found in each of six NFS individuals infected with this helminth.

Nematodes were found in 91.9% of the NFSs examined and included 5 species, all belonging to the family Anisakidae. Since it was not possible to distinguish the females of *Pseudoterranova decipiens* and those of *P. azarazi* (Yamaguti et Arima, 1942), we combined quantitative data for both species. They appeared to be the most prevalent group of nematodes (P = 84.2%) with the highest mean abundance of 5.5. The highest mean intensity among the nematodes in a single NFS was 265 specimens of *Anisakis simplex* (Table 2). However, the majority of *A. simplex* specimens (75.6%) were in larval stages. *Phocascaris cystophorae* (Goto and Ozaki, 1930) was the rarest nematode species (P = 5.5%) (Table 2).

Four recognized trematode species had a comparatively low total prevalence of 32.3%. *Nanophyetus salmincola* was found in one seal but with an impressive quantity of 1540 specimens. *Phocitrema fusiforme* was the most common trematode species with maximum infection intensity of 410 specimens in one seal followed by *G. ubelakeri* and *A. zalophi* Price, 1932 (Table 2).

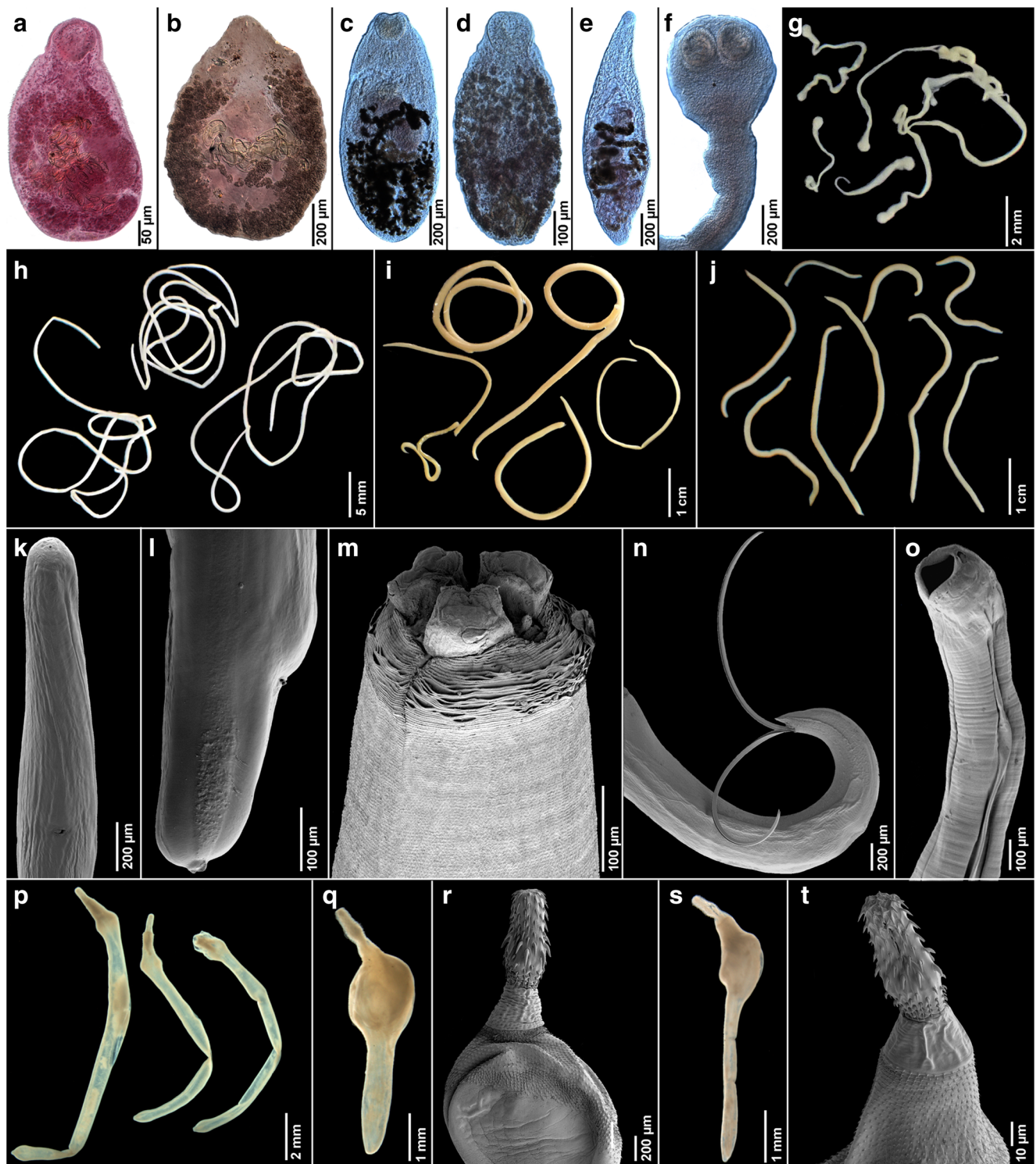


Fig. 1 Microphotographs of the helminths from northern fur seals *Callorhinus ursinus*. **a–e** Trematoda. **f, g** Cestoda. **h–o** Nematoda. **p–t** Acanthocephala. **a** *Apophallus (Pricetrema) callorhini*. **b** *Cryptocotyle (Ciureana) delamurei*. **c** *Galactosomum ubelakeri*. **d** *Nanophyetus salmincola*. **e** *Phocitrema fusiforme*. **f, g** *Anophryocephalus ochotensis*. **h, k, l** *Acanthocheilonema odendhali*. **i** *Pseudoterranova* spp. **j, o**

Uncinaria lucasi. **m, n** *Contracaecum osculatum* s. l. **p** *Bolbosoma nipponicum*. **q, r** *Corynosoma cameroni*. **s, t** *Corynosoma strumosum*. **a, b** Material from type series collected by M. Yurakhno from Commander Archipelago. **c–t** Newly obtained material from St. Paul Island, Alaska, USA. **a–f** Light microscope photographs. **k–o, r, t** SEM photographs

With 3 species found, tapeworms were the least diverse group. While tapeworms lacked diversity, they were the most

prevalent group of gastrointestinal helminths, found in 98.5% of examined seals. Comparatively high prevalence and

abundance of tapeworms were observed in both diphyllbothriids, *Adenocephalus pacificus* and *D. tetrapterum* (Siebold, 1848), while the tetrabothriidean *Anophryocephalus ochotensis* Delyamure et Krotov, 1955, was found in 4 of the 651 seals (Table 2).

According to the prevalence values, 5 groups of parasite species were established (Fig. 2): dominant species ($P > 70.1\%$), subdominant species ($30.1\% < P < 70\%$), common species ($10.1\% < P < 30\%$), rare species ($1.1\% < P < 10\%$) and occasional species ($P < 1.0\%$). The tapeworm *A. pacificus* and the nematodes *Pseudoterranova* spp. were found in more than 80% of the seals; thus, they were dominant species. The group of subdominant species contained two anisakids (*C. osculatum* and *A. simplex*) and the diphyllbothriid *D. tetrapterum*. The group of common species had the trematode *P. fusiforme* and 4 acanthocephalans of the genus *Corynosoma* (*C. strumosum*, *C. similis*, *C. semerme* (Forssel, 1904) and *C. villosum* (Van Cleave 1953)). The group of rare species was comprised of 5 species: anisakid nematode *Phocascaris cystophorae*, trematodes *G. ubelakeri*, *A. zalophi* and acanthocephalans *Bolbosoma nipponicum* (Yamaguti, 1939) and *C. validum* (Van Cleave 1953). The acanthocephalans *C. cameroni* and *C. alaskensis* (Golvan, 1959), the tapeworm *Anophryocephalus ochotensis* and the trematode *N. salmincola* were found in less than 1% of hosts and were considered as occasional NFS parasites (Fig. 2).

Analysis of relative abundance (RA) revealed that the most commonly occurring species *A. pacificus* and

Pseudoterranova spp. were also the most abundant, composing almost 61% of the total number of helminths (Table 2, Fig. 2). The nematode *A. simplex* and the trematode *P. fusiforme* had the highest relative abundance other than *A. pacificus* and *Pseudoterranova* spp., at 9.2% and 7.3%, respectively (Fig. 2). Five dominant and subdominant species constituted more than 80% of the gastrointestinal helminth individuals found in this study. The total proportion of the other 14 species, including the trematode *N. salmincola*, was less than 20% (Fig. 2).

Temporal and spatial differences within the component community

We tested possible rookery/year effects on species composition and structure of NFS gastrointestinal helminth community using the Linear Model Evaluation with a Randomized Residual Permutation Procedure (Table 3; see “Material and methods” section for details).

We found significant differences between the three studied years ($p = 0.0096$) but not among the five rookeries ($p = 0.84$). No significant interaction was found between the effects of year and rookery ($p = 0.15$; i.e. year-to-year trends seem not to be different in different rookeries). Statistically significant differences in gastrointestinal helminth infections in NFS from the 5 rookeries for the entire period (2012–2014) were not found ($p = 0.84$). All of the studied effects explain a small piece of the total variation shown by R^2 estimates (Table 3).

Fig. 2 Prevalence (%) and relative abundance (%) of gastrointestinal helminth species found in northern fur seals *Callorhinus ursinus* on St. Paul Island, Alaska. Black bars—dominant species; dark grey bars—subdominant species; grey bars—common species; light grey bars—rare species; white bars—occasional species

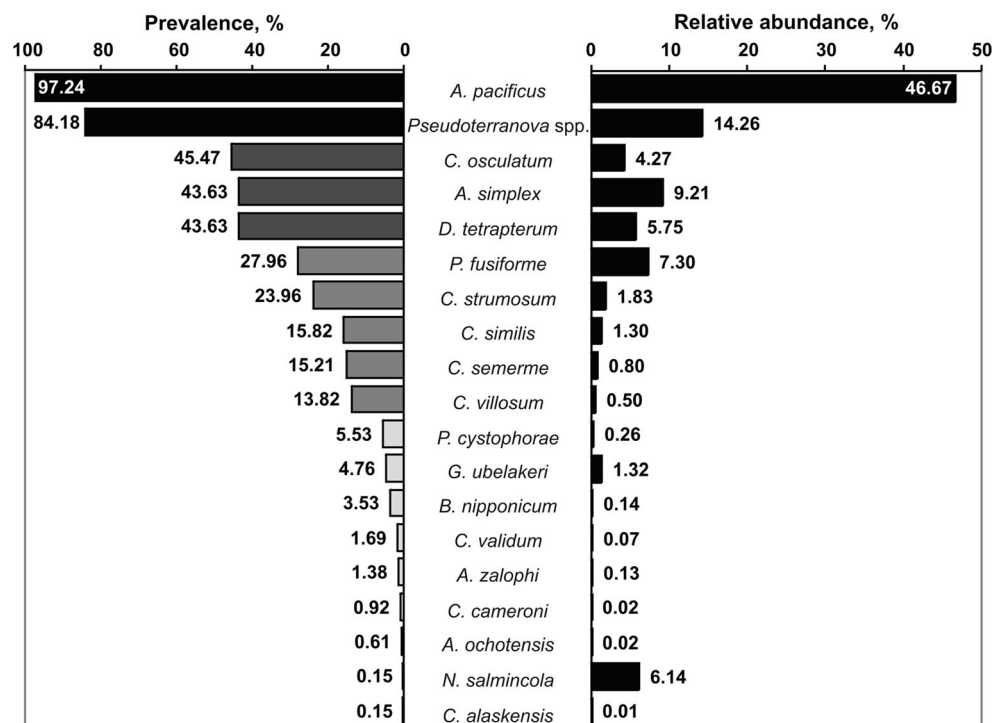


Table 3 Analysis of variance, using residual randomization for the effects of year and rookery on gastrointestinal helminth communities found in northern fur seals *Callorhinus ursinus* on St. Paul Island, Alaska, USA

Effect	Df	SS	MS	F	R^2	p value
Rookery	4	3294	823.4	0.66	0.005	0.84
Year	2	7568	3784.1	3.04	0.012	0.01
Rookery \times Year	7	8722	1246.0	1.30	0.014	0.15
Residuals	637	612,187	961.0		0.969	
Total	650	631,771			1.000	

Df — degrees of freedom, SS — sums of squares, MS — mean squares, F — Fisher's statistics for testing, R^2 partial coefficients of determination

Characterization of gastrointestinal helminth infracommunities

All examined NFSs were infected with helminths. The species richness ranged from 1 to 10 species (mean 4.3; median 4) and the abundance ranged from 1 to 452 helminth specimens (mean 36.2; median 29). The median value of the species richness in the infracommunities (4 species) was observed in the largest number of host individuals: 133 (20.4%), while the maximum number of helminth species (10) was observed only in three NFS individuals (0.5%) (Fig. 3).

Co-occurrence of gastrointestinal helminths in the infracommunities

The correlations between the numbers of the gastrointestinal helminths of different taxa and their p values are given in

Table 4 and illustrated in Figs. 4 and 5. The matrix in Fig. 4 shows the correlations for each pair of selected helminths taxa. The areas of the filled circle sectors show the absolute value of corresponding correlation coefficients. The correlations of co-occurrence for most gastrointestinal helminth species found in NFSs are low (Table 2, Figs. 4 and 5). Most of the correlation coefficients are close to zero ($-0.12 < r_S < 0.12$; $p > 0.05$) indicating that there is no evidence for a relationship between the frequencies of gastrointestinal helminths. For some pairs of taxa (see Fig. 4), there is a slight positive correlation (i.e. two taxa of helminths were more often observed together than in the case of random infection: the heavier the parasite infection in an NFS with one species, the greater chance this seal will be infected with another species). Significant negative correlations between the abundance of any helminth species were not found. The maximum positive correlation in our data was found for acanthocephalans *C. similis* and *C. strumosum* ($r_S = 0.37$) and for nematodes *C. osculatum*, *Pseudoterranova* spp. and the tapeworm *D. tetrapterum* (r_S is about 0.3). The correlation was slightly lower between these two groups; correlation for *A. simplex* and *B. nipponicum* was also significant (Table 4, Figs. 4 and 5). Therefore, the higher the abundance of one of these 7 gastrointestinal helminth species (see Fig. 5), the higher the chance to find another species in the same individual seal.

Analysis of the relations between infections by separate gastrointestinal helminth species and their co-occurrence revealed the absence of significant correlations for a number of pairs of helminth species (Fig. 4). Co-infection of NFSs with acanthocephalans *C. strumosum*, *C. similis* and nematodes of the genus *Pseudoterranova* were the most common. These species were found together in 58 NFSs (8.9%).

Fig. 3 Frequency distribution of gastrointestinal helminth species richness in northern fur seals from St. Paul Island, Alaska

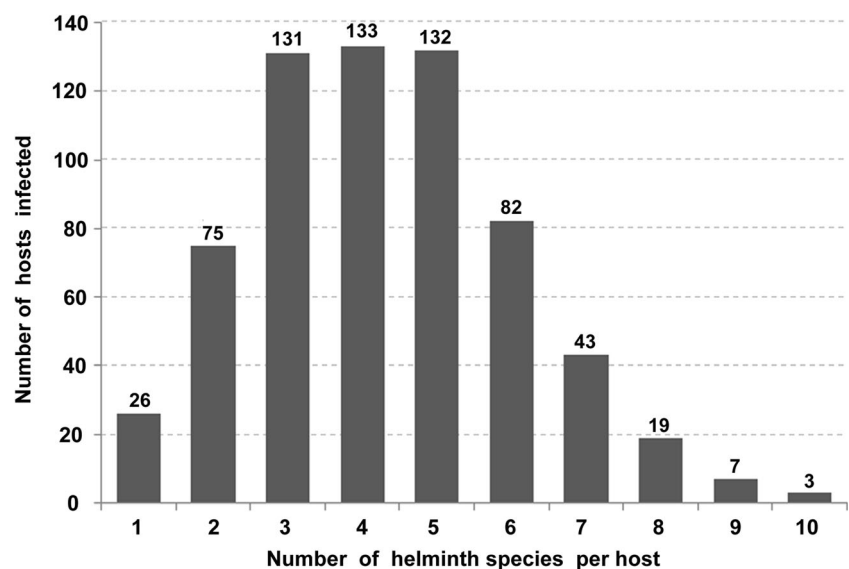


Table 4 The estimates and *p* values for correlations between the numbers of gastrointestinal helminths of different taxa in the infracommunity of northern fur seals *Callorhinus ursinus* on St. Paul Island, Alaska, USA. The Spearman's correlation coefficients are in the upper triangle, *p* values are in the lower triangle. The significant values ($|r_{sij}| > 0.12$, $p < 0.05$) are shown in bold

	Asi	Cos	Pse	Pey	Apa	Dte	Aoc	Pfu	Aza	Gub	Cst	Cvi	Cva	Csi	Cse	Cca	Bni
Asi																	
Cos																	
Pse																	
Pey																	
Apa																	
Dte																	
Aoc																	
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Aza																	
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Cvi																	
Cva																	
Csi																	
Cse																	
Cca																	
Bni																	

Asi — *Anisakis simplex*, Cos — *Contracaecum osculatium*, Pse — *Pseudoterranova* spp., Pey — *Phocascaris cystophorae*, Apa — *Adenocephalus pacificus*, Dte — *Diphyllobothrium tetraapterum*, Aoc — *Anoplocephalus ochotensis*, Pfu — *Phocitrema fusiiforme*, Aza — *Apophallus zalophi*, Gub — *Galactosomum ubelakeri*, Cst — *Corynosoma strumosum*, Cvi — *Corynosoma villosum*, Cva — *Corynosoma validum*, Csi — *Corynosoma similis*, Cse — *Corynosoma semerne*, Cca — *Corynosoma cameroni*, Bni — *Bolbosoma nipponicum*

Fig. 4 The correlations between the numbers of gastrointestinal helminths of different taxa in the infracommunity of northern fur seals *Callorhinus ursinus* on St. Paul Island, Alaska. Aoc—*Anophryocephalus ochotensis*, Apa—*Adenocephalus pacificus*, Asi—*Anisakis simplex*, Aza—*Apophallus zalophi*, Bni—*Bolbosoma nipponicum*, Cca—*Corynosoma cameroni*, Cos—*Contraecaecum osculatum*, Cse—*Corynosoma semerme*, Csi—*Corynosoma similis*, Cst—*Corynosoma strumosum*, Cva—*Corynosoma validum*, Cvi—*Corynosoma villosum*, Dte—*Diphyllobothrium tetrapterum*, Gub—*Galactosomum ubelakeri*, Pcy—*Phocascaris cystophorae*, Pfu—*Phocitrema fusiforme*, Pse—*Pseudoterranova* spp. See text for the details

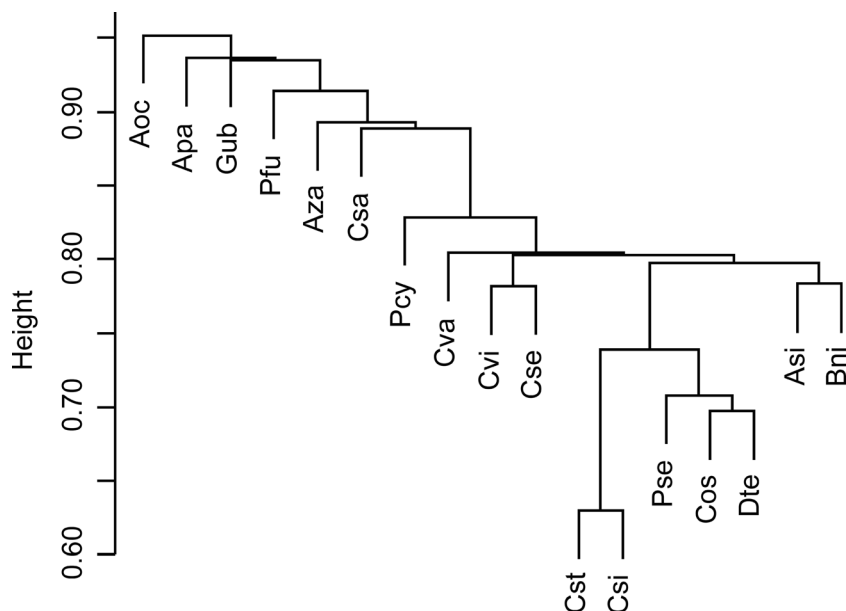
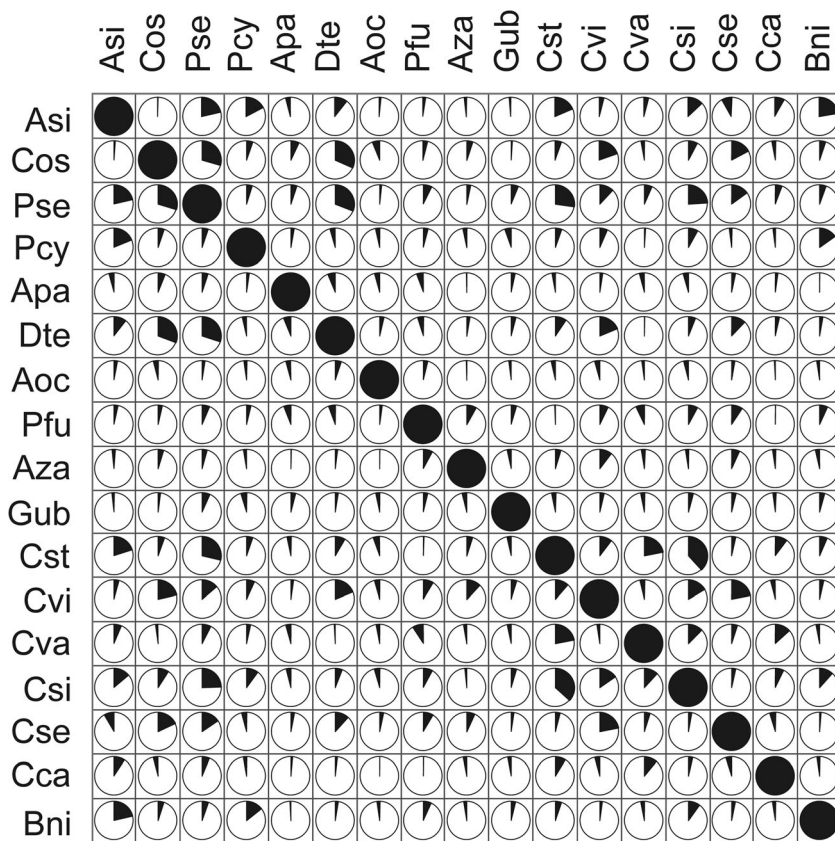


Fig. 5 Hierarchical cluster analysis for correlation between numbers of different gastrointestinal helminths infecting northern fur seal *Callorhinus ursinus* specimens. Aoc—*Anophryocephalus ochotensis*, Apa—*Adenocephalus pacificus*, Asi—*Anisakis simplex*, Aza—*Apophallus zalophi*, Bni—*Bolbosoma nipponicum*, Cca—*Corynosoma cameroni*, Cos—*Contraecaecum osculatum*, Cse—*Corynosoma*

semerme, Csi—*Corynosoma similis*, Cst—*Corynosoma strumosum*, Cva—*Corynosoma validum*, Cvi—*Corynosoma villosum*, Dte—*Diphyllobothrium tetrapterum*, Gub—*Galactosomum ubelakeri*, Pcy—*Phocascaris cystophorae*, Pfu—*Phocitrema fusiforme*, Pse—*Pseudoterranova* spp.

Discussion

Our study presents the first comprehensive analysis of the gastrointestinal helminth community in NFSs based on examination of a large number of seals within four consecutive years. Before our project, only fragmented studies of different groups of parasites were carried out on St. Paul Island (Neiland 1961; Keyes 1965; Perry and Forrester 1971). The diversity of helminth species found in NFSs on the Pribilof Archipelago was considered to be low and amounted to only 12 species (see Yurakhno 1998). According to our data, at least 23 species of helminths (Tables 1 and 2) and 2 species of nasal mites parasitize NFSs on St. Paul's Island. Four species (trematodes *G. ubelakeri* and *N. salmincola*, and the acanthocephalans *C. alaskensis* and *C. cameroni*) were newly documented in NFSs in our previous and present surveys (Kuzmina et al. 2012, 2018; present study). Moreover, the examination of numerous freshly collected well-fixed material with molecular data allowed us to synonymise two species of tapeworms, *Diplogonoporus violettiae* Yurakhno 1986 and *Diphyllobothrium (Diplogonoporus) tetraapterum* (Kuzmina et al. 2015). Additionally, the collected material and molecular data allowed for the invalidation of all other diphyllobothriids reported in NFSs, with exception of *A. pacificus* (Kuzmina et al. 2015; Hernandez-Orts et al. 2018).

Ionita et al. (2008) misidentified acanthocephalan *Corynosoma semerme* collected from NFSs from St. Paul Island as *C. obtuscens* (now synonymised with *C. australe*). This was recently confirmed also by molecular methods (Lisitsyna et al. 2019). The validity is unclear of two trematode species, *Apophallus callorhini* and *Cryptocotyle delamurei*, described from a single seal from Bering Island, the Commander Archipelago, by Yurakhno (1986, 1987), as these parasites have not been reported since they were initially described. We hypothesize that the heterophyid *A. callorhini* could be synonymous with *A. zalophi*. The original description of *A. callorhini* was based on 13 exemplars. This species was distinguished from the congeners due to the larger size of its mouth, abdominal suckers, pharynx and spines which are not suitable discriminating characters for species of this group. Moreover, several metrical characters of *A. zalophi* reported in the original description of *A. callorhini* were incorrect (see Yurakhno 1986). The original description of opisthorchid *C. delamurei* was based on 25 specimens and was distinguished from other species of the genus *Ciuraena* (= *Cryptocotyle*) by a smaller length and width of the body, in addition to smaller oral and genital suckers, testes, ovary and eggs (Yurakhno 1987). The differentiation of *C. delamurei* and *C. jejuna*, both rarely reported from NFSs (see Table 1), was not performed. We examined several specimens of both species from the type series (Fig. 1), but their low quality did not allow us to confirm or synonymise these species. New material from the type locality is necessary for the final decision.

Ecological studies of NFS parasites have been carried out only on the Commander and Kuril Archipelagoes of the Russian North Pacific, where several hundred NFSs were examined and 14 helminth species were reported (Delyamure 1961; Yurakhno and Taikov 1986; Yurakhno 1998). However, our study allowed us to compare our data from the Pribilof Archipelago only with the data from the Commander Archipelago, in the Bering Sea (see fig. 1 in Kuzmina et al. 2015). The NFS populations from the Pribilof and Commander Archipelagos may partially overlap in the Bering Sea during feeding migrations (Sokolov 1998; Gentry and Kooyman 2014). Therefore, similar parasite fauna could be expected in both populations. A comparison of the parasite community structure of these two Archipelagos allowed the following conclusions.

The tapeworm *A. pacificus* was the most dominant helminth species in both populations ($P = 92.5\%$ in Commander population and $P = 97.2\%$ in Pribilof population); *D. tetraapterum* was confirmed only in the Pribilof population. Onchoproteocephalidean larvae of *Scolex pleuronectis* were found in only 9.6% of the NFSs from the Commander Islands (Yurakhno 1998). *Pseudoterranova* spp. were the most common nematodes in both populations ($P = 70.12\%$, intensity 2.7 in the Commander population; $P = 84.2\%$ in the Pribilof population). *Phocascaris cystophorae* was more common in the Commander population ($P = 50.3\%$, intensity 2.6) than in the Pribilof population (Table 2). Moreover, *C. osculatum* was an extremely rare species in the Commander population ($P = 1.07\%$) in contrast to its prevalence in the Pribilof population ($P = 45.5\%$) (Table 2). *Uncinaria lucasi* was the most pathogenic parasite of NFS pups on the Pribilof Archipelago causing high pup mortality (Olsen 1958; Lyons 1963). However, its prevalence has decreased in recent decades from around 90% in 1978, to 6–10% in 1999 and 3–5% in 2007–2011 (Lyons et al. 2011, 2012, 2014). This species was found to be quite rare on the Commander Archipelago (prevalence < 1%) (Yurakhno 1998). We also documented the dramatic decline in the intensity of anisakid nematodes compared with the data collected on St. Paul Island 30–40 years ago (Keyes 1964; Spraker et al. 2003), which may be associated with changes in NFS diet as well as a decline in NFS populations in the North Pacific during last decades (Kuzmina et al. 2014; Gelatt et al. 2015).

Acanthocephalans were the most diverse group of helminths in this study with 7 species found. Half of NFSs were infected with acanthocephalans, mainly with *C. strumosum* (Table 2). In the Commander population, 5 species of acanthocephalans were found. *Corynosoma villosum* was the most common species (prevalence 58%), while *C. strumosum* was found only in 10.7% of seals (Yurakhno 1998). According to Delyamure (1955) and Delyamure et al. (1976), the main hosts of *C. strumosum* are spotted seals (*Phoca largha*) and bearded seals (*Erignathus barbatus*). During the last several

decades, global climatic change and decreasing ice habitats in the North Pacific has led to a dramatic decline of spotted and bearded seal populations, especially near Alaskan shores (Boveng et al. 2009; Cameron et al. 2010). The decline in the population of spotted and bearded seals could lead to significant changes in the helminth community in NFSs, including acanthocephalans.

Trematodes also were a diverse group of helminths including four species in the Pribilof population; almost one third of NFSs were infected with *Phocitrema fusiforme* (Table 2). The Commander population harboured three species, *P. fusiforme*, *A. callorhini* and *Ciureana delamurei* (Table 1), with a low prevalence of 1.07% (Yurakhno 1998). Our present study was performed more than 30 years after the observations on the Commander population (Yurakhno and Taikov 1986; Yurakhno 1998) and several climatic and environmental factors including a decline of fish stock or decrease of NFS population mainly influenced the noted differences (Trites 1992; Towell et al. 2006; Sinclair et al. 2008; Allen and Angliss 2015; Gelatt et al. 2015).

In our study, tapeworms were the most prevalent group found in almost all NFSs examined ($P = 98.5\%$), followed by nematodes (91.9%), acanthocephalans (47.3%) and trematodes (32.3%).

The two dominant taxa, tapeworm *A. pacificus* and nematodes *Pseudoterranova* spp., composed almost 61% of the total number of helminths, while the total proportion of the 10 rare and occasional species was less than 5%. It could be that these dominant gastrointestinal helminth species have a pathogenic influence on NFS health (Keyes 1965; Yurakhno and Taikov 1986), while the effects of rare and occasional species are less impactful. Still, the results of multi-year studies on NFS mortality did not reveal any significant effects of parasites and other pathogens compared with effects of starvation, emaciation and trauma (Spraker and Lander 2010).

We suggest that there is a common pattern for infections in NFSs with helminths, which varies from rookery to rookery and from year to year due to environmental factors. However, the effect of year and rookery on the distribution of helminth taxa was very small (Table 3). Absence of significant differences among different rookeries indicated that the gastrointestinal helminth community on St. Paul Island may be considered as a whole, even though the feeding grounds of NFSs from different rookeries are separated (Robson et al. 2004; Sterling and Ream 2004; Zeppelin and Ream 2006). The positive correlation ($r_s = 0.37$) between the abundance of the acanthocephalans *C. similis* and *C. strumosum* may be explained by similarities in their life cycles and, consequently, simultaneous infection of NFSs with both species. Similarly, a positive correlation for the nematodes *C. osculatum* and *Pseudoterranova* spp. may be due to their similar transmission methods (Delyamure 1955; Yurakhno 1998). Interestingly,

the occurrence and abundance of the cestode *D. tetrapterum* positively correlated with those of *C. osculatum* and *Pseudoterranova* spp. However, information on the life cycles and transmission of these parasites in the Bering Sea ecosystems is insufficient; several parasites may use the same fish species as their intermediate host. Complex parasitological studies of marine mammals and fish, as well as different groups of invertebrate intermediate hosts, are needed to explain these correlations.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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